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Address: P.O. Box 123, Moruya, NSW, Australia.

A re-appraisal of the systematic position of *Trichastoma poliothorax* (Timaliinae, Muscicapidae)

by C. F. Mann, P. J. K. Burton & I. Lennerstedt

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INTRODUCTION

Aside from the Grey-chested Illadopsis *Trichastoma poliothorax*, whose systematic position is here in question, the genus *Trichastoma* contains 18 species (Deignan 1964). Of these, 11 are Asiatic, ranging from the Himalayas south and east through Burma and the Malay Peninsula to Indonesia and the Philippines. The other 7 are African, ranging from W. Africa to Sudan, south to Malawi and Angola. All live close to the ground in dense undergrowth. They are smallish babblers, generally brown or rufescent above, and greyish, whitish, pale rufous or orange below, often with some scaling on head and underparts. In some the colour of the crown contrasts with the mantle. In all but *cinereiceps* the rictal bristles are very pronounced; and *cinereiceps* also differs from all the others in having a very short tail.

The systematic position of *poliothorax* has never been satisfactorily settled. The species was originally described as *Alethe poliothorax* (Reichenow 1900) and both Chapin (1953) and later Hall & Moreau (1970) suggested that it may be a turdine. Ripley (1952), in his treatment of the Turdinae, omitted it. Deignan (1964) gives no particular reason for its inclusion in the Timaliinae. Most recent authors agree, though expressing reservations, on placing it in the genus *Trichastoma* (or *Malacocincla*, now merged with *Trichastoma*) in the subfamily Timaliinae (Chapin 1953, Hall & Moreau 1970, Mackworth-Praed & Grant 1960). C. F. M. has noticed a superficial resemblance of the bird in the hand to *Modulatrix stictigula*. (It should perhaps be mentioned that Benson & Irwin (1975) have removed *orostruthus* from *Phyllastreptus* and added it to *Modulatrix*, a previously monotypic genus.)

Our investigations have utilised skin specimens of all species of *Trichastoma*, and spirit specimens of the following: *T. tickelli*, *malaccense*, *rostratum*, *bicolor*, *albipectus*, *fulvescens*, *pueveli* and *poliothorax*.

DISTRIBUTION, HABITAT AND HABITS

White (1962) gives the distribution of *T. poliothorax* as 'Fernando Po, southeast Nigeria at Obudu Plateau, Cameroon Mt., Kupe and Bamenda in Cameroons, northeast Congo from west of Lake Albert to Ruwenzori and Mt. Kabodo, west Kenya at Mt. Elgon and Lerundo in Kavirondo'. To this can be added the Impenetrable Forest, Uganda (Keith *et al.* 1969) and the South Nandi Forest, and adjacent parts of the Kakamega Forest (Ripley & Bond 1971). In netting operations in Kenya and Uganda over a period of 5 years, C. F. M. only found it in Kakamega and South Nandi Forests of western Kenya, at altitudes of 1560–1700 m: its distribution within the area was very patchy. Zimmerman (1972) spent a total of 9 months in the Kakamega Forest and never found it.

The species *poliothorax* is a scarce denizen of wet, montane forest, from 1500 m (900 m on Mt. Cameroon) to 2400 m, found on or near the ground. Like all in the genus, *Trichastoma* is a great skulker and is rarely observed except when flying across a path or captured in a mist net. Fortunately there was a small resident population in the main study area used by C. F. M., who thinks that it spends more time on the ground and less time higher in the undergrowth than most *Trichastoma*, but because of its fondness for deep cover observations on free living birds are few. Its presence is often revealed only by its distinctive call (see below).

PLUMAGE

Whereas other members of *Trichastoma* have a rather coarse-feathered, somewhat untidy appearance, *poliothorax* is a finer, neater bird, with closer, denser feathering and much less obvious rictal bristles, and with a distinctive colour pattern, being mahogany-rufous above contrasting with dark grey underparts, which incline to white on the throat and centre of belly.

Of 4 immature birds, one from northeast of Lake Tanganyika (Chapin 1953), one from Dikume Balue, Cameroons (British Museum, examined by C. F. M.), and 2 captured by C. F. M. at Kakamega Forest, none had a typical spangled turdine immature plumage. The Cameroons specimen differs from the adult in having rufous-brown tips to the grey chest feathers, brown iris (red-brown in the adult), an orange-yellow gape and an unossified skull. The 2 Kakamega birds differed from adults in being less chestnut and more gingery on the sides of the face, rump and lower back, and showed a certain amount of olive on the grey chest. The irides were dirty-brown and the gape soft and yellow. In none of the 4 specimens is there any mottling above. Apparently no very young birds have ever been seen, and the nest and eggs are unknown. However, C. W. Benson suggests that a spangled plumage, if it exists, might be worn for a very short time and could easily escape notice. He quotes the example of *Pogonocichla stellata* in Malawi, for which he knows of only a single record of a spangled bird, whereas the olive immature dress is frequently seen.

BILL AND TONGUE

Bill form is extremely similar in all species of *Trichastoma*, including *poliothorax*. Rictal bristles are well developed in *Trichastoma*, less so in *cinereiceps* and even less well developed in *poliothorax*.

The tongue of *poliothorax* is distinctive. It narrows sharply from the base,

and the sides are strongly infolded, forming a 'U'-shaped cross-section. It is very narrow for most of its length, and has a frayed, brush-like tip. In the other species of *Trichastoma* examined the tongue is broad and flat, though also with a somewhat frayed tip.

Bill and tongue lengths are given in Table 1. The tongue is longest, relative to the bill, in *poliothorax*, only *malaccense* approaching it closely in this respect.

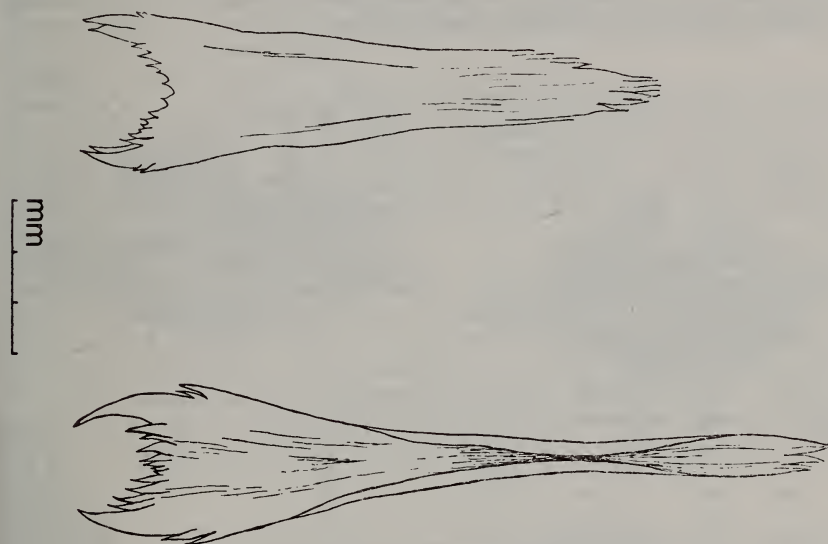


Fig. 1. Tongues of *Trichastoma albipectus*, above, and *T. poliothorax*, below.

CRANIUM

As the specimens available were spirit ones, a detailed osteological comparison was not undertaken. However, the skull of *poliothorax* differs noticeably from others of *Trichastoma* in its general shape (Table 1), being wider relative to its length than in other members of *Trichastoma*, and also more tapering, i.e. relatively narrower in front of the orbits than behind. An additional point of some interest is the angle made at the intersection of the

TABLE 1

Quantitative data on head morphology in the genus *Trichastoma*, including *poliothorax*.

	<i>tickelli</i>	<i>malaccense</i>	<i>rostratum</i>	<i>bicolor</i>	<i>pyrrhopterum</i>	<i>albipectus</i>	<i>poliothorax</i>
Cranium length from junction of nasal and jugal (A)	21.3	23.3	21.9	23.8	23.5	22.4	23.2
Greatest cranium width posterior to orbit (B)	16.0	16.2	15.9	18.0	17.6	16.9	16.0
Greatest cranium width anterior to orbit (C)	7.1	7.8	7.0	8.4	6.7	6.5	9.4
Anterior: Posterior width ratio C/B	0.44	0.48	0.44	0.47	0.38	0.38	0.59
Width: Length ratio C/A	0.33	0.33	0.32	0.35	0.28	0.29	0.41
Bill length, from junction of nasal and jugal (D)	15.7	16.1	17.1	19.2	14.0	14.7	17.0
Tongue length (E)	11.3	13.2	12.6	13.8	11.0	11.0	14.2
Tongue: Bill ratio E/D	0.72	0.82	0.74	0.72	0.79	0.75	0.84
Postorbital ligament/jugal angle	92°	92°	95°	90°	90°	87°	112°

post-orbital ligament and the jugal bar. The angle in the dorsal anterior quadrant of the intersection (Table 1) is considerably greater in *poliothorax* than in other members of *Trichastoma*.

JAW MUSCLES

Substantial differences between *poliothorax* and other *Trichastoma* species were noted in the structure of M. adductor mandibulae externus and M. pterygoideus. The terminology used here for subdivisions of these muscles is that employed by Richards & Bock (1973).

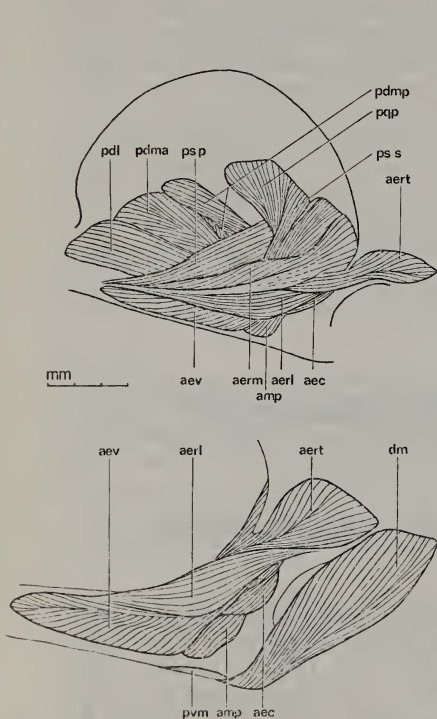


Fig. 2. Jaw musculature of *Trichastoma albipectus*. Dorsal view, upper; lateral view, lower.

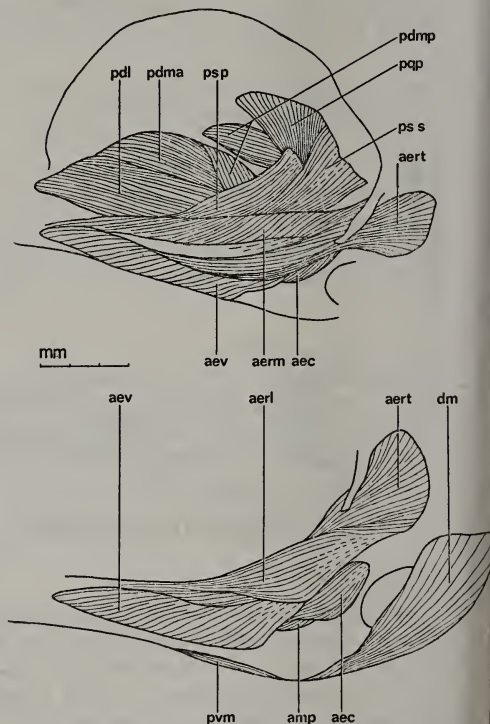


Fig. 3. Jaw musculature of *Trichastoma poliothorax*. Dorsal view, upper; lateral view, lower.

Key:—

- aec — M. adductor mandibulae externus caudalis.
- aeri — M. adductor mandibulae externus rostralis lateralis.
- aerm — M. adductor mandibulae externus rostralis medialis.
- aert — M. adductor mandibulae externus rostralis temporalis.
- aev — M. adductor mandibulae externus ventralis.
- amp — M. adductor mandibulae posterior.
- dm — M. depressor mandibulae.
- pdl — M. pterygoideus dorsalis lateralis.
- pdma — M. pterygoideus dorsalis medialis anterior.
- pdmp — M. pterygoideus dorsalis medialis posterior.
- pqp — M. protractor quadrati et pterygoidei.
- psp — M. pseudotemporalis profundus.
- pss — M. pseudotemporalis superficialis.

M. adductor mandibulae externus (M.a.m.e.)

T. poliothorax: M.a.m.e. rostralis temporalis has a very small area of origin, and shows no clear separation from the lateralis portion. M.a.m.e. rostralis medialis and rostralis lateralis are closely united and extend equally far anteriorly.

Other species: M.a.m.e. rostralis temporalis extends markedly further posteriorly at the origin, and is clearly separated from the lateralis portion by a well marked groove. M.a.m.e. rostralis medialis extends less far anteriorly than M.a.m.e. rostralis lateralis, and is slightly separated from it anteriorly, giving the impression of a distinct slip.

M. pterygoideus (M.pt.)

T. poliothorax: M.pt. dorsalis lateralis is separated medially by a clear groove from M.pt. dorsalis medialis anterior, but does not overlap it. M.pt. dorsalis medialis posterior has origin along the full length of the anterolateral and posterolateral surfaces of the pterygoid. The fibres of M.pt. dorsalis medialis anterior fan out evenly from their insertion on the medial surface of the mandible as seen in dorsal view.

Other species: The medial edge of M.pt. dorsalis lateralis overlaps M.pt. dorsalis medialis anterior substantially, though still leaving much of it exposed to dorsal view. M.pt. dorsalis medialis anterior is smaller than in *poliothorax*, its anterior origin being confined to the posterior half of the anterolateral surface of the pterygoid, though posterior fibres originate along the whole length of the postero-lateral surface. M.pt. dorsalis medialis anterior shows distinct bipinnate structure in dorsal view, with fibres diverging from a raphe of insertion—most strongly so in *tickelli* and least well defined in *bicolor*.

FEET

The pads and the folds on the feet have already been studied in a number of European passerine species by Lennerstedt (1973, 1974, 1975 a, b, c) and his methods and terminology are followed here. One specimen of *poliothorax* (Kenya) and singles of *Trichastoma tickelli* (Malaya), *T. malaccense* (Malaya), *T. rostratum* (Malaya), *T. bicolor* (Malaya), *T. pyrrhopterum* (Kenya), *T. albipectus* (Zaire) in the spirit collection of the British Museum were studied.

The plantar surface of the foot has pads (extensive raised areas) and folds (narrow raised areas) which are separated by furrows. Pads and larger folds have papillae, whereas the smaller folds may lack them. The papillae in the pads are mostly smaller and more pointed than the papillae in the folds, indicating that the papillae in the pads are regularly in contact with the substrate. The pads, folds, furrows and papillae appear during the first half of embryonic life (Lennerstedt 1973) and they are as characteristic as other morphological features, e.g. those of the skeleton.

The contour of the pads and folds and the profile of the claws were drawn on paper using a stereo microscope with a camera lucida apparatus. The paper was cut along the contour of the pad and the size of the pad was calculated from the weight of the piece of paper. The papillae in the pad were counted and the average size of the papillae in the pad was calculated. This is the size of the base of the papillae, not of the top of the papillae, the structure of which may vary with season (Lennerstedt 1975c).

The 6 typical species of *Trichastoma* studied have a similar pattern of pads and folds in the feet and the minor differences between them can be explained as individual variation within any of the species (Lennerstedt 1975a). However, *poliothorax* differs substantially from all the others, and for the following treatment can be compared with *T. rostratum* representing the 6 species of *Trichastoma*.

The pads and folds in *T. rostratum* and *poliothorax* are shown in Fig. 4. Eight areas with differences between the 2 species (A-H) are described in Table 2.

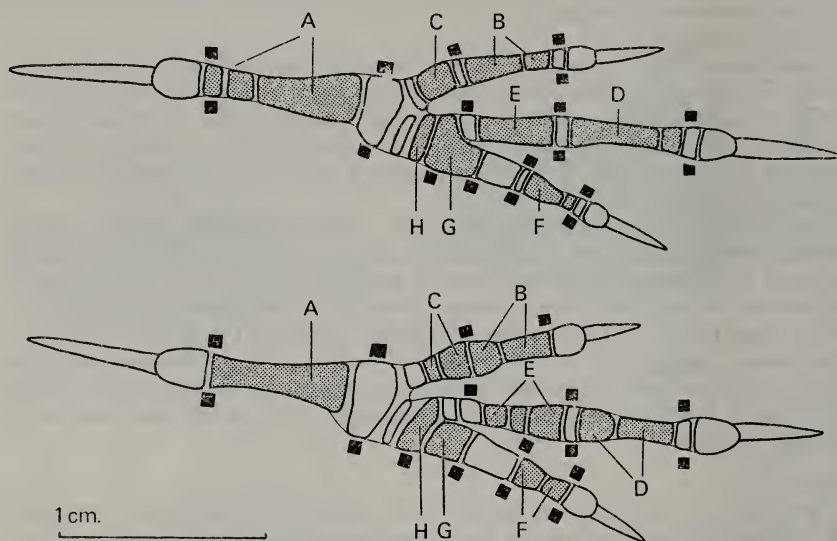


Fig. 4. Plantar surface of the foot in *T. rostratum*, upper and *T. poliothorax*, lower. Pads and folds referred to in Table 2 are shaded and lettered.

In general *rostratum* has more folds than *poliothorax*. This implies that the pads in *poliothorax* lie closer to each other, particularly at the joints. A functional implication of this may be that the digits in *rostratum* may be more strongly curled around small twigs than in *poliothorax*.

The following pads are divided into 2 in *poliothorax*: pad II:2, III:2, III:3, and IV:2. One of the parts is broad and the other more narrow. This means that the parts of the pad have become specialised. A similar division does not occur in *rostratum*.

The basal phalanges of the anterior digits differ between the species. *T. rostratum* has phalanx II:3 and III:4 substantially shorter than phalanx II:2 and III:3 respectively; *poliothorax* has phalanx II:3 and III:4 about similar length to II:2 and III:3 respectively. *T. rostratum* has phalanx IV:5 longer than IV:4, whereas *poliothorax* has the 2 phalanges about equal length. Almost nothing is known about how passerines use the phalanges as levers in grasping twigs and in standing on the ground. The different proportions of the phalanges, however, must imply differences in the ability to perform these tasks.

TABLE 2

Comparison of foot pads and folds in *T. rostratum*, including *poliothorax* (see Fig. 4).

*T. rostratum**T. poliothorax*

DIGIT I

A. Pad I:2 narrowing, ended with 2 folds.

Pad I:2 is narrowest in the middle part; no fold distal to the pad.

DIGIT II

B. Pad II:2 narrowing distally, ended with 2 folds.

Pad II:2 divided into one broad basal and one narrow distal part; no fold distal to the pad.

C. Pad II:3 has typical muscicapid form; basal to it is a narrow fold.

Pad II:3 is comparatively small, the pad lying near joint II:2/3; basal to it are 2 comparatively large folds.

DIGIT III

D. Pad III:2 narrowing distally, ended with 2 folds.

Pad III:2 divided into one broad basal part and one narrow distal part, ended with one fold.

E. Pad III:3 is long, rectangular.

Pad III:3 divided into one broad distal part and 2 narrow basal parts with papillae as in the folds.

DIGIT IV

F. Pad IV:2 narrowing distally, ended with 2 folds.

Pad IV:2 divided into 2 about equal large parts; no fold distal to the pad.

G. Pad IV:4 is longer than phalanx IV:4, lying ventral to phalanx IV:4 and joint IV:4/5; pad IV:4 is joined to folds at phalanx III:4.

Pad IV:4 is shorter than phalanx IV:4, lying ventral to it.

H. Fold IV:4/5 displaced basally, lying ventral to distal part of phalanx IV:5; the fold has papillae as other folds.

Fold IV:4/5 lies ventral to joint IV:4/5 and it has grown together with folds at phalanx III:4. The fold has papillae similar to those in the pads.

The differences in the length of phalanges correspond to differences in pads and folds and their relation to the phalanges in digits III and IV (see G and H, Table 2). Joint IV:4/5 in *rostratum* lies at the basal part of pad IV:4, but in *poliothorax* the joint lies at the fold basal to the pad, and this fold is enlarged.

A noticeable difference concerns pad II:3. *T. rostratum* has a typical II:3 with a narrow fold basal to it, whereas *poliothorax* has a comparatively small pad II:3, lying close to the joint, and 2 large folds basal to the pad. The distal of the 2 folds is probably a separated part of pad II:3. The structure of pad II:3 in *poliothorax* is analogical to the differentiation of pad II:2, III:2 and III:3.

For 8 pads, the size of pad was measured, the number of papillae counted, and the average size of papillae calculated (Table 3). The 6 species, represented

TABLE 3

Size of pad, and number and size of papillae in 7 species of *Trichastoma* including *poliothorax*.

Species	Pad size mm ²	Papillae number	Papillae size, mm ²
<i>tickelli</i>	32.6	437	0.075
<i>malaccense</i>	33.1	248	0.143
<i>rostratum</i>	33.3	383	0.088
<i>bicolor</i>	34.5	338	0.101
<i>pyrrhopterum</i>	35.6	307	0.116
<i>albipectus</i>	31.3	317	0.097
<i>poliothorax</i>	40.7	339	0.115

Note: Papillae size is calculated as the mean of eight pads, not as the mean of the figures in the table.

by *T. rostratum* in Fig. 4, with a similar pattern of pads and folds, are easily compared as every pad and fold in one species has an equivalent in any of the other species. The values of *poliothorax* are calculated on pads, many of which have different positions in the foot, so that they are not closely comparable with the other species, but they are of value as general information on these features.

The comparison of the species shows that *poliothorax* has the largest total area of pads. This may be explained by the lack of certain folds and the corresponding expansion of pads. In all species, the total number of papillae varies considerably, from about 250 to about 380, *poliothorax* lying within this range of variation. The average size of papillae varies according to the number of papillae, from 0.14 to 0.075 mm². In *poliothorax* the papillae are comparatively large, averaging 0.115 mm². In the number and size of papillae *poliothorax* does not deviate from *Trichastoma* species. However, *poliothorax* had pad II:2, III:2, and III:3 divided into one broad and one narrow part. The broad parts, lying close to the joint, have papillae of about 0.10 mm², whereas the narrow parts have substantially larger papillae of about 0.16 mm². The circumstances in pad IV:2 are similar. The basal part of pad IV:2 has papillae of about 0.08 mm² and the distal part of about 0.13 mm². Similar differentiation between basal and distal parts of the pad, though undivided, may be suggested in *Trichastoma* species, but the differences are insignificant. The differentiation of pad II:2, III:2, III:3, and IV:2 into 2 parts in *poliothorax* is thus accompanied by a substantial differentiation in the size of papillae.

There are many similarities between *Trichastoma* and *poliothorax*. The 6 species of *Trichastoma* show only a minor variation in the length of the digits. The lengths in *rostratum* are exactly the same as in *poliothorax*. The curvature of the claws was studied only in *rostratum* and *poliothorax*. In these 2 species, the corresponding claws have exactly the same length and curvature.

In *rostratum* the long and narrow pads are comparable to those in certain species of Turdinae, e.g. the European Robin *Erithacus rubecula* or the Redstart *Phoenicurus phoenicurus*. The 2 folds near the distal joint in the 4 digits are features found in many species of Sylviinae. *T. rostratum* is thus comparable to species of Muscicapidae which include the ground in their habitat. On the other hand the pattern of pads and folds in *poliothorax* does not occur in typical Turdinae or Sylviinae. Instead it is comparable to those found in wagtails, genus *Motacilla*, and pipits, genus *Anthus*, of the family Motacillidae. This does not imply phylogenetic relationship between *poliothorax* and species of the family Motacillidae, only that the pads and folds are adapted to the same type of substrate and the same way of using the digits.

The conclusion from this comparison is that the 6 *Trichastoma* species, with *T. rostratum* as a described example, are typical arboreal species of Muscicapidae which have certain adaptations to live on the ground. Although *poliothorax* also shows adaptations to live on the ground, the differences between this species and *rostratum* are profound. They indicate that *poliothorax* has an evolutionary history which has for a long time been separated from that of *Trichastoma*. The similarities between *poliothorax* and *Trichastoma* probably depend upon convergence and adaptations to similar habitats.

VOCALISATIONS

Members of the genus *Trichastoma* usually reveal their presence by their conspicuous calls. Some duet, or sing in groups. This behaviour is recorded by C. F. M. for *T. rufipennis*, *fulvescens* and *pyrrhopterum*, and Chappuis (1975) adds *cleaveri* and *poliothorax*.

T. poliothorax has a loud, almost ringing, 7-9 note call, a common form of which could be transcribed as 'chee-wee-woo, wee-woo, wee-woo', with the second, fourth and sixth syllables stressed. It has an almost oriole-like quality. Chappuis (1975) states 'Phrase genre Turdidae ou Oriolidae.'. C. F. M. has never recorded group singing or duetting in this species, but Chappuis (1975) has published a group song from Mt. Cameroon.

Three species of *Trichastoma* (*fulvescens*, *pyrrhopterum* and *rufipennis*) sympatric with *poliothorax* in western Kenya produce fairly simple warbling songs, usually with a leader, and one or two others contributing chuckles, rattles and other harsh notes. A fourth species, *albipectus*, has a far-carrying slow series of 2-4 whistles, usually preceded by a barely-audible warbling-chuckle. All 4 have harsh 'scurrying' alarm notes, as has *poliothorax*.

A recording of *Ptyrticus turdinus* (Chappuis 1975) was considered by C. F. M. to recall that of *poliothorax*, but is clearer and louder, and even more oriole-like.

DISCUSSION AND CONCLUSIONS

Differences between *poliothorax* and typical members of *Trichastoma* in plumage and vocalisations are perhaps of no great significance, but they lend weight to our conclusion that *poliothorax* should be removed from *Trichastoma*. The unspotted immature plumage suggests that it is not a member of the Turdinae, although this is not a constant feature of the subfamily, as *Modulatrix* (Benson & Irwin 1975) and *Neocossyphus* (specimens in British Museum examined by C. F. M.) apparently have unspotted young.

Having found no close relative for the species we therefore erect a new genus, which until further evidence is available, we feel should remain within the Timaliinae:

Kakamega, gen. nov.

Type species: *Kakamega poliothorax* (Reichenow).

Diagnosis: A smallish oscine (mean weight of 16 of both sexes, 36.38 g) with the general characteristics of the tribe Pellorneini of the sub-family Timaliinae. It differs from the typical members of the genus *Trichastoma* as follows:

- (a) rectal bristles much reduced;
- (b) tongue longer relative to bill, and of 'U'-shaped cross-section;
- (c) skull shape wider in relation to length, and more tapering;
- (d) the angle in the dorsal anterior quadrant of the intersection of post-orbital ligament and jugal bar considerably greater (112° compared to $87-95^\circ$);
- (e) in the structure of the jaw muscles *M. adductor mandibulae externus* and *M. pterygoideus*.
- (f) in the structure of the foot pads II:2, III:2, III:3, and IV:2.
- (g) in the lengths of basal phalanges in the anterior digits. (In the pattern

of pads and folds it also differs from all studied members of Sylviinae and Turdinae.)

(h) feathering finer and closer than *Trichastoma*.

(i) Vocalisations.

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- Addresses:* C. F. Mann, City of London Polytechnic, Old Castle Street, London E.1.
Dr. P. J. K. Burton, British Museum (Natural History), Tring, Hertfordshire, England.
I. Lennerstedt, Zoological Institute, University of Lund, Sweden.

Vocal mimicry in the lark *Mirafra hypermetra* as a possible species-isolating mechanism

by Françoise Dowsett-Lemaire & R. J. Dowsett

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The lark *Mirafra hypermetra* is usually considered to be a good species by ornithologists in East Africa (e.g. Williams 1963: 180), but no justification for this appears to have been published. Hall & Moreau (1970: Map 7) treat *m. hypermetra* and *M. africana* as separate species, though without great conviction. In a review of *M. africana* (*sensu latu*) White (1960: 8-9) has